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# Discussion on Alternative Hypotheses

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# Discussion on alternative hypotheses

B. Adefris

Without siding with either of the hypotheses, I want to cite an example of our experience of a very serious Desert Locust upsurge in 1967–8 in eastern Africa. We thought that this began somewhere on the Egyptian border in May 1967 (Rainey & Betts, this symposium, figures 1 and 2, appendix, C19), the next generation came and bred in the Sudan, and the next generation kept on coming south, into the province of Eritrea (Hemming *et al.*, this symposium, figure 3). During 1967 and 1968 we were invaded by locusts on such a scale that we thought that not only our organization, but even all the organizations together, could never have dealt with them. Our problem was to try and control those locusts, wherever they were; and how much that cost didn't matter. In fact, we were able to spray some 700000 l of chemical in a matter of one year. In Eritrea we were able for the first time to control the locusts in the highlands, spraying them as they climbed the escarpment in the Asmara area for example; they stopped longer in the highlands because it was colder there. Thereafter we have sprayed again, at rates of 60 to 70 thousand litres per year between 1971 and 1973 for example, to try and keep the locusts down at their lowest level.

R. J. V. Joyce

I don't really think it makes very much difference which of the hypotheses is correct from the control point of view, but perhaps this is because I don't understand the controversy and, like Mr Yeo, I have been away from locust control for a long time. A lot of emphasis is placed on the role of gregarization; but how important in fact is this process of gregarization in the Desert Locust? As I thought was accepted some 10 years ago, the Desert Locust can learn to gregarize in a matter of hours, or overnight; it does not require several generations, as seemed to be indicated by Mr Hemming: who emphasized how even solitary locusts behave in a gregarious manner in oviposition. With regard to morphometrics, as I understand the situation, the solitarious morphometrics can be developed by gregarious populations under certain conditions of high temperature, and the morphometric characteristics of a locust population give no information on the behaviour of that population but only on its previous history. So, as I see it, we can ignore gregarization; we have a process of concentration, followed by multiplication: or is multiplication a pre-necessity for concentration? In practice, although a lot of information can be obtained about the areas over which rain has fallen, where opportunities therefore occur for breeding and multiplication, the areas over which rain falls are very large in relation to the area which is going to be covered by hopper bands – or by the insects in general; even under plague conditions with very heavy gregarious breeding, not more than 3–4% of the total area which is infested is covered by hopper bands. Now control in an area in which multiplication is occurring is only really practicable if the hoppers are concentrated, because the areas are too big to treat scattered populations. From the control point of view, whether concentration follows multiplication, or multiplication follows concentration, one has to concentrate on discovering those conditions under which concentration occurs. One of these situations is of course the concentration of adult locusts in wind fields; the other opportunity is concentration of hoppers, in suitable vegetation; and both requirements can only be met by appropriate aerial survey.

G. B. Popov

While I agree with Professor Vernon Joyce, and Mr Yeo that there is a considerable amount of common ground between the alternative hypotheses, there are also differences, which in practical terms are of paramount importance. One major difference is that one hypothesis lays stress on the importance of gregarious and the other on the importance of non-gregarious populations during recessions between plagues. The practical importance of this distinction is that the methods, tactics and strategy of survey, detection and control of the two types of populations are quite different: a matter of vital importance to such regional and international control organizations as OCLALAV and DLCOEA represented among us by their directors M. Abdallahi and Ato Adefris who, I am sure, must attach very considerable importance to this particular problem.

I wonder if the speakers would like to comment on the practical implications of their hypotheses individually and perhaps in concert, in terms of a practical strategy which could be recommended to the organizations responsible for the control of regional migrant pests.

R. C. Rainey and Elizabeth Betts

In reply to George Popov, we agree that there are indeed significant differences between the practical implications of these two hypotheses. We see his as envisaging that Desert Locust populations between plagues exist for extended periods at densities (and perhaps in numbers) too low to merit control; this would, accordingly, indicate the location of conditions conducive to concentration, multiplication and gregarization as a primary survey objective. In the other, we envisage recession populations large enough and at densities at least intermittently high enough to merit immediate control, as continuously present and on the move within the distribution area; this would accordingly indicate more continuous contact with these populations as the primary objective of improvements in reconnaissance and control.

From the point of view of those with responsibilities for Desert Locust control, our continuity hypothesis emphasizes a continuing need (and scope) for remaining alert for the abrupt reappearance of populations meriting immediate control, up to several months and many hundreds of kilometres away from the time and place of disappearance of such populations. Thus for example even in 1966, with Desert Locust populations at their lowest overall level for at least 28 years, breeding in the Tibesti area of Chad (with control operations against concentrations of hoppers and fledglings over an area of 110 km$^2$: our report W16) provided the basis of a D.L.I.S. warning which was cabled by Ann Lumley to Libya in September, and was followed by the discovery in November of further concentrations of late-instar hoppers and fledglings against which control was undertaken over an area of some 60 km$^2$ near Wau el Khabir in south Libya, 400 km north of Tibesti (W18). These were the two largest Desert Locust populations actually found by control organizations anywhere over a period of 10 months.

In the context of our hypothesis of continuity of mobile populations, OCLALAV's 'zones of gregarization', for example, would represent favoured halting-places for potentially dangerous populations on the move, rather than independent starting-points for future trouble. We appreciate fully the recognition and characterization of such areas as important contributions toward the more frequent contacts with mobile populations that we consider particularly necessary.





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C. F. Hemming, G. B. Popov, J. Roffey and Zena Waloff

1. The task facing national and regional Desert Locust organizations during recessions is to prevent the formation of the large gregarious populations characteristic of plagues. Thus the controversy over whether plagues arise from a more or less continuous line of high-density populations, or as a result of successful breeding by populations which fluctuate between lesser and greater densities is of more than academic interest, for it has important practical implications for the tactics and strategy of plague prevention.

2. In their 'continuity hypotheses' Dr Rainey and Miss Betts consider it probable that most, and possibly all, records of gregarization follow only a temporary dissociation of the populations concerned, and that during dissociation periods these populations survive as the larger and more important non-swarming populations.

3. But when we examine their appendix we see that in all three Desert Locust regions there were gaps between confirmed records of swarming populations long enough for the production of several successive generations, and that at times the gaps overlapped in all three regions. Rainey & Betts themselves state that in the postulated genealogical chain joining the swarms of the preceding plague to swarms of 1967–8 upsurge there were 'gaps of up to 18 months' (in other words, of 4–5 successive generations) between confirmed (or unequivocal) records of swarming populations. Thus the distribution in time of such records certainly does not suggest the continuity of the gregarious state.

4. As to the suggested links, in their figure 1, between successive swarming populations (regardless of whether these are confirmed or unconfirmed) or, when these are absent, with other populations designated as the 'main', Rainey & Betts admit that these have been postulated simply by analogy with earlier swarm migrations. It is, however, well known that while such suppositions may be plausible for some movements they are much less so for others. There is in fact a great deal of variation in migration routes from year to year, so that the occurrence of a particular movement on one occasion does not imply that it will occur on the next. Yet no attempts appear to have been made to assess the probability of any of the postulated movements in relation to contemporary wind-fields. Thus in this respect also the 'swarm continuity' hypothesis cannot be regarded as adequately substantiated.

5. Moreover, no consideration has been given to possible derivations of the listed populations from the numerous unlisted low-density populations known to have been present and breeding and migrating in the recession area at the time. This has not been done even in such specific cases as the 1967 Tamesna outbreak (Hemming *et al.*, § 3) where some of us witnessed, at first hand, the gregarization of the progeny of an initially widely scattered low-density population.

6. During recessions the great majority of reports refer to populations at low densities and direct observations by ourselves and a number of other field observers and the analysis of biogeographical data strongly support our hypothesis that Desert Locust outbreaks result from concentration of such low-density populations into areas which favour multiplication and gregarization. The low-density populations reaching such areas may be derived from several widely separated sources (Hemming *et al.*, § 3 *b*). We accept that populations involved in outbreaks may sometimes include locusts which had been partially gregarized in their life-time; this is to be expected in a mobile polymorphic species whose populations are liable to mingle during displacements or on arrival at breeding sites. But we find no evidence that their participation is a necessary pre-requisite for the development of an outbreak.





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7. Somewhat rarely during recessions population levels are sufficiently high for there to be a continuity of high-density populations for two or three generations. The best example of which we are aware comes not from the 1963–7 recession but from the more recent (and continuing) recession, when some of the second generation of swarms produced in India and Pakistan in the summer of 1973 (Hemming *et al.*, § 3*b*) moved west, overwintered and laid as swarms in the spring of 1974. But such occurrences are exceptional, and all available evidence indicates that most recession swarms are (*a*) small in size and locust numbers and (*b*) they are unstable and liable to become dispersed. It is to be expected that their members would then fly by night and merge with contemporary low-density populations which may greatly exceed them in locust numbers.

8. Again, because plague upsurges are characterized by the build-up of populations over extensive areas, the wide range of recession populations initially present or drawn into these areas could easily comprise, or rapidly acquire, some partially gregarized components. But the most significant feature about plague upsurges is not the phase status of the initial populations; it is the repeated occurrence of widespread conditions favouring cumulative increases in absolute numbers with concomitant gregarization over several successive generations.

9. Turning to the practical implications of our hypothesis, we regard the breeding stage as the most important strategically, because it is at this stage that recession populations are: (i) most likely to be most concentrated (Hemming *et al.*, § 3); (ii) liable both to increase in absolute numbers and to become more gregarious; and (iii) most static and easiest to locate within readily recognizable breeding areas, which at any one time occupy only comparatively restricted portions of the seasonal zones. In fact the rapid location and survey of current breeding areas and control within them already forms the basis of plague prevention operations of Desert Locust control organizations.

10. But because practical difficulties do arise in implementing the recommended policy in parts of the recession area (some of which remain unsurveyed), we also recommend that research be undertaken on developing any methods which could lead to more effective and efficient ways of monitoring and controlling large recession populations. We have already mentioned the use of satellite imagery in detecting potential Desert Locust breeding sites, and referred to ground and air radar for monitoring airborne locusts (Hemming *et al.*, § 5). However, because flying locusts during recessions may reach sprayable densities only when concentrated by wind convergence, investigations are required to establish whether such concentrations are sufficiently predictable and lasting to provide worthwhile targets.

R. C. Rainey and Elizabeth Betts

We welcome our C.O.P.R. colleagues' recognition both of the general need for a strategy taking advantage of situations in which recession populations are most likely to be concentrated (by environmental factors as well as by their own behaviour), and also of the special potentialities of airborne radar in reconnaissance for night-flying locusts under recession conditions. From experience (R. C. R.) of the use of this equipment in Canada, in conjunction with Doppler wind-finding by the same aircraft (Schaefer § 3*c*; see also Greenbank, Schaefer & Rainey 1979), we would emphasize that it is this particular combination of facilities which now provides so powerful a tool for systematically seeking and quantitatively assessing concentrations of airborne insects.

On § 2 of the comments of Chris Hemming and our other colleagues, we would emphasize that we envisage temporary dissociation as commonly followed by gregarization again *within* the lifetime of the individuals concerned.

On § 3, we envisage most of the gaps between appearances of swarming populations as merely losses of contact, to an extent no more than is to be expected from experience of the problems of reconnaissance and of the nature of the information available. It is difficult to accept as pure coincidence the repeated records of swarms or bands at intervals of not many months throughout the longest recession, and so often at appropriate times and places to suggest links with other reports, even though a number of these reports could not be individually confirmed.

When learning to forecast under recession conditions, we found ourselves obliged to treat 'unconfirmed' reports of locusts systematically, for the complete confirmation of an individual swarm report is often not physically possible, not only in a recession but also during plague periods, when confirmation of most individual swarm reports is neither sought nor needed. Reports in the field can cover a complete spectrum of credibility, ranging from that of a swarm one has been inside oneself, to the unambiguously false report of the alleged eye-witness subsequently found to have been hundreds of kilometres away at the time of his report. Between these extremes can remain all intermediate shades of doubt, on many of which no final yes/no verdict may ever be possible despite the most strenuous of efforts. To us the only logical procedure was to maintain all appropriate reservations in respect of each report (and in particular to retain the term 'unconfirmed' as recording doubt on the part of the person forwarding the report), but nevertheless to keep on the record (with all these reservations) every report which has not been unambiguously disproved. For the purposes of our 1963–7 list of locust populations, and our figure 2, we had to decide, necessarily arbitrarily, where to draw the line across the continuous spectrum of credibility of the field reports. We chose to omit altogether single unconfirmed reports without supporting evidence, but to consider a second and independent (though still individually unconfirmed) report from the same area and period as circumstantial evidence in support of the first and justifying its inclusion

Furthermore, in assessing the development of locust situations, either in real time (for forecasting) or retrospectively (for research), we have attempted to take full account of the relationships in space and time of all available locust reports, more comprehensively and systematically than appears to have been done previously. In doing so, it has been necessary to accept the inevitably iterative nature of the process involved in subsequently considering potential links: the spatial and temporal relationships of a locust report can provide valuable though circumstantial evidence *both* of the possible authenticity of the report *and* of the possibilities of links with other reports, but cannot provide conclusive *proof* of either. At the same time, it is also necessary to take full account of the manner in which the value of circumstantial evidence rapidly increases with the number of independent items of circumstantial evidence on the same point.

These considerations are in our view sufficiently important (and perhaps unfamiliar) to merit a detailed example, conveniently provided by the series of unconfirmed locust reports in the north Somali peninsula during October to December 1966 (our C17), which our colleagues felt 'could not be substantiated' (Hemming *et al.*, § 4). A small immature swarm was reported in this area on 20 October 1966, with a second, independent report of locusts within 50 km of this position on the same day; a swarm was reported at Mait on 21 November, and a group of locusts near Bosaso, also on the north Somali coast, on 1 December. Admittedly a DLCOEA ground party did investigate the first two of these reports on the spot, within three days, and with negative results. However, from personal experience (R.C.R.) of chasing swarms, in this





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area and elsewhere, one could not accept this as unambiguous evidence of their absence. Furthermore, these reports had been preceded by a herd-boy's report of hopper bands between Hargeisa and Awareh on 16 October, at a stage picked out from specimens as third or fourth instar. This would correspond to an inferred laying date of about 10–18 September, a period which included a spell of unusual and widespread rains, reported for example on 13 September at Burao and Diredawa as well as at Hargeisa, which recorded a September total of 123 mm (more than twice the average for the month). Moreover, locusts are known to have been present in considerable numbers elsewhere in the northern region of Somalia earlier in the season, with a confirmed report (our C16) of scattered locusts appearing near Las Anod in June, flushed over a distance of 65 km at densities up to 11 per 90 m, and extending over an area of at least 2600 km$^2$.

We considered the cumulative weight of these items of circumstantial evidence as sufficient to justify the inclusion of the October/December series of reports in our list and diagram. In Arabia, on the other hand, there were no locusts reported anywhere at all during August, September and October 1966; and, while we fully accept that they are not likely to have been totally absent (hence the '?' at about 60° E in our original diagram), we would be reluctant to derive the subsequent Arabian locust build-up entirely from such hypothetical parents, as our colleagues do (§ 4), without envisaging any possibility of participation by some of the locusts reported in the Somali peninsula, particularly under the influence of the Gulf of Aden cyclone of November 1966.

In their discussion of the upsurges of 1940–1 in the western region, of 1949 in the eastern region (§ 4), and of early 1967 in the Sahara (§ 3*a*), our colleagues somewhat similarly omit any mention even of the known and confirmed earlier gregarious populations (Waloff 1966) respectively of January 1940 in Tibesti and of August 1948 in Pakistan, or of the known concentrations in Libya and Mali in November 1966 (our W17 and 18).

On their § 4, we attach indeed great importance to the study of contemporary wind fields in interpreting locust situations (and forecasting their development); and the links suggested in our diagram took full account of our experience of having followed the current daily synoptic weather charts of the whole Desert Locust area over the 6 year period since we introduced the preparation and use of these charts at the Desert Locust Information Service in 1961. On more than twenty occasions in the course of the period covered by our diagram we had in fact directed attention, in the regular monthly DLIS situation summary and forecast of those days, to particular features of contemporary wind fields which we suggested as likely to prove to have been important in this respect, such as the cyclone of November 1966.

On § 5, we have indeed omitted, for convenience, the listing and consideration of a number of the low-density locust populations known to have been present over this period, because they failed to satisfy our stated criterion of providing evidence of locust numbers of the order of millions. But our presentation of the 1967 Tamesna upsurge in the diagram duly includes – on this criterion – the presence of the low-density population in October before the gregarization of its progeny in November.

On § 6, more than 50 years of reasonably documented Desert Locust history have not produced a single upsurge without previous known gregarious populations available for participation. If their participation is not a necessary prerequisite then coincidence must again be strong.

On § 7, similarly well documented sequences of a number of generations of high-density locust populations were recorded in the same areas of India and Pakistan at similar times of year in 1964–5 (our E 6–7), and provided unexplained though admitted exceptions to the generalizations of our colleagues concerning the qualitative and quantitative characteristics of the gregarious populations of recession periods. Moreover, their statement that 'the initial concentration of locusts was due not to low-level wind-convergence...but to the behavioural responses of the locusts to the ground environment' does not appear to be supported by the meteorological information which is provided. Thus in Rajasthan in 1973 the timing of the first recorded appearance of hopper bands, in numbers, suggests that laying at markedly increased densities (i.e. by parents which had just been concentrated) not only immediately followed the occurrence of the depression but also took place in the areas in which the heavy rains of the depression fell. It is not clear why the powerful wind-convergence needed for the production of these rains should have been considered as a negligible factor in the concentration of the locusts, relative to the effects of behavioural responses on which no information is provided in this case.

On § 8, we would certainly agree on the unimportance of the phase status of the initial populations in an upsurge, or indeed subsequently, since in this species, the fundamental behavioural phase characters have been found, as Vernon Joyce has already pointed out, to change in a matter of hours, both in the laboratory (Ellis 1959) and in the field (Rainey 1962). This incidentally makes the use of the term 'non-swarming', re-introduced in 1967 for recording any low-density population, somewhat misleading for this species.

On § 9, we do not agree that the breeding stage is necessarily the most important strategically. In addition to the fact that it is often considerably shorter than the total flying life of the adult in the field:

- on § 9 (i): what matters is not the maximum concentration – per square metre – which certainly occurs in the egg stage, but the extent of the area which it is necessary to search at any one time. During plague periods this can at times be very much smaller for adults, e.g. in the convergence zone of the Somali horn, than for the corresponding hoppers, as Vernon Joyce and DLCOEA have exploited; and we would suggest taking account of a similar possibility during recession periods, particularly if and when appropriately instrumented aircraft become available for systematically seeking and searching zones of wind-convergence;
- on § 9 (ii), gregarization occurs also during the adult stage, to an extent which Uvarov (1966) considered had been insufficiently appreciated; adult concentration may occur on a scale and almost certainly at a speed much greater than is possible in the non-flying stages;
- on § 9 (iii), during a plague period it has been possible, even away from any convergence zone, to achieve by daytime air reconnaissance a more complete coverage of a major infestation of flying swarms than was ever possible of hopper bands; and the airborne radar and wind-finding instrumentation now in existence offer comparable possibilities for the night-flying (and other) adult populations of recession periods.

On § 10, the suggestion that during recessions flying locusts may reach sprayable densities only when concentrated by wind-convergence, like that of the less cohesive behaviour suggested as characteristic of recession swarms, has not so far been supported by any direct observations, of the kind which established during plague periods that the cohesion and identity of individual swarms were not only regularly maintained in some areas, over periods of weeks, but were regularly lost in other areas, sometimes daily.





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D. L. Gunn

As the oldest British locust worker still active, I have been trying to get into perspective the two conceptions of the course of Desert Locust upsurges leading to outbreaks. Of course, Miss Zena Waloff has worked on locusts for far longer than I have, but she is younger than me and still deeply involved. Naturally one has to start with Uvarov's phase theory.

This theory was originally of great value in showing the range of morphological variation of locusts and identifying the species when they did not look like locusts. It was of immense value in public relations. I wonder if it has not now almost ceased to be useful, because its terminology is used in such a way as to obscure fundamental meanings. Perhaps it is counter-productive because its terminology is used in such a way as to dress up and stereotype events and therefore to obscure what is important in what actually happens. Of course, to revise and still more to abandon beliefs that have been held for most of one's working life is difficult and to do so smacks of disloyalty. But our greater loyalty should surely be to truth and to practical help for people. The irrelevance of morphological phase status in Desert Locusts in forecasting populations and in control programmes has been increasingly realised for some years (Rainey 1962). Since 1960 (Gunn 1960*a*, *b*) the overriding importance of what have been called 'mere numbers' has become widely recognized (e.g. Hemming *et al.*, this symposium).

I have therefore tried to interpret the paper by Hemming *et al.* without using phase terminology, so as to help in comparing their ideas and policy with those of Rainey & Betts.

We have, first, the classical idea of the origin of locust plagues. After generations of small and thin populations, enough rain falls to permit sufficient vegetation to grow to enable the population to increase, aided by the now familiar wind mechanisms for bringing the migrating locusts to the favourable places, mechanisms worked out and demonstrated to the hilt by Rainey (1963).

Here we come to the first point of conflict. Hemming *et al.* consider that this initial upsurge in population (and I use the word *upsurge* rather differently from them) characteristically comes from scattered populations with no necessary recent history of crowding or large numbers.

I do not consider that we can exclude the possibility of this happening. Nevertheless, evidently the upsurge can reach a given level of numbers a generation or more sooner if the immigrant population is larger, as it would be if the product of recent swarming. The question then is: what usually actually happens?

It is not only swarms that are obviously coherent that migrate in daytime; large numbers of locusts may move almost as secretly in daytime as those that migrate at night. My experience in Somaliland in April 1950 is perhaps relevant. Breeding had been extensive, intensive and successful. I was there to experiment on methods of hopper control (Gunn 1952) but eventually had to stop because the hoppers were too old to take bait, not because of lack of patches and bands of hoppers which had certainly been crowded. Leaving by road from the coast at Berbera southwestwards to the airfield at Hargeisa on 27 April, a journey which took about 3 h, I kept looking out for locusts leaving on the wind, in the same direction as ourselves, and saw nothing that could ever be called a swarm; but very high up, the whole time the glitter of wings could be seen from single locusts visible only close to the sun. If that was an emigrant swarm, it was an exceedingly thin one – and a very extensive one. When these locusts bred in their turn, they may well have become concentrated again – certainly very concentrated and successful breeding was recorded during May 1950 in many parts of this region, including the Giggiga and

Diredawa areas to the southwest of my sightings. In this case there appear to have been locusts becoming temporarily diffuse between their very concentrated hopper life and their concentrated laying as adults.

On the other hand, a swarm that was certainly coherent when we followed it for 18 days in 1945, when it was becoming progressively more yellow, could not be discovered as a swarm in the laying area. Yellow mating and laying locusts were scattered widely, the colour indicating that they had come from a swarm.

There is a large collection of relevant data. Aided by that enormous collection of information about the Desert Locust, initiated by Uvarov and managed by Miss Waloff for many years, Rainey & Betts have made a persuasive case for continuity, for an upsurge being so favoured by an initially large immigrant population that that is likely to be the usual course of events. Continuity of rather numerous populations which sometimes become diffuse transitorily is not proved – and Rainey & Betts do not claim that it is – but they provide a logical framework which is worth examining not only for its truth but also for its practical value. The criticism by Hemming *et al.* of the continuity hypothesis because of the breaks in continuity in figure 2 seems at first to be telling, more telling in any case than their own hypothesis in place of it; but of course it is expecting too much to require that no breaks shall occur in reporting as distinct from breaks in actual continuity in nature.

In discussing planning of control operations, Hemming *et al.* emphasize the well-known importance of exceptionally good local rainfall, which Rainey showed long ago generally occurs in circumstances which bring migrant locusts to the very same localities. The wind brings the locusts and when they are favoured by good rains and good vegetation, they stop, which can produce considerable increases in area density if the favourable locality is small; after successful breeding, there will presumably be further increases in local density which, in the first generation of an upsurge, may not be important except in the total numbers surviving. The very early identification of such temporarily favourable areas is vitally important. Hemming *et al.* rightly hold that monitoring by all possible means to reveal occupation of sites in those areas is essential, but this should be combined with forecasting of migration of populations, perhaps on the continuity hypothesis but in any case in the most successful way.

Now on the Rainey & Betts continuity hypothesis, a population breeding successfully but not itself numerous enough to be likely to lead directly to damaging swarms, should be controlled because it is part of a chain that should, and could profitably, be broken. If continuity forecasting combined with satellite pictures of rained-on areas and possibly aircraft searches indicate or even suggest possibility of an upsurge, then control should surely be actively considered.

On both sides of the argument, it is agreed that large populations during recessions should be dealt with. What counts as *large* remains open. The emphasis in practice has to be initially on finding out where rain has fallen; Rainey & Betts add to that forecasting on continuity theory.

Once an upsurge presents itself for control, to prevent an outbreak the techniques require pilots who are trained to use them, are familiar with their use in practice, and well disciplined. Attacks on the kind of upsurges predicted by continuity hypothesis and spotted by growth of green vegetation can provide training and familiarization during relatively quiet times. Without work, in quiet times air crews and ground crews are apt to become demoralized and equipment to deteriorate and to be found to be unsuitable when the testing time comes; familiarization in a regular programme could help to reduce these risks.

As to the future, as far as I can see a decision between the two hypotheses – or a decision on the frequency with which each holds – will be exceedingly difficult on the basis of purely local observations. Can any observer of an extensive favourable breeding area ever guarantee that no insensible reinforcements or unnoticed swarm immigrations have arrived? Can any follower of a small recession swarm ever guarantee that his swarm made more than a slight difference to a resident and insensibly reinforced population? Perhaps local observations could be really valuable only after numerical population assessments of Desert Locusts over enormous areas. These present big problems and solutions should be sought for them.

J. S. Kennedy, F.R.S. (*Imperial College, London*)

Both J. Roy and M. Abdallahi have made it clear that their strategy for Desert Locust plague prevention is the good old Uvarovian one of locating outbreak areas and concentating control measures there. The impression one got from Dr Gunn's opening statement was that for the Desert Locust the invasion area and the recession area were not very different in extent, which would seem to discount the idea of concentrating on outbreak areas; but the important distinctions are those between breeding areas, recession area and outbreak areas. The outbreak areas are much smaller than the non-swarming breeding area, which is itself less than half the size of the invasion area, so that the ratio of invasion area to outbreak area is something like thirty to one. Thus even with this intractable, diffuse, unpredictable, nomadic Desert Locust, it seems to me that the basic Uvarovian principle has not changed, and in fact looks healthier in relation to the Desert Locust than it did in the 1950s and 1960s when the migration of non-swarming locusts and the shifting locations of outbreak areas cast doubt on it.

D. L. Gunn

The conception of outbreak areas grew out of the nineteenth century American idea of permanent breeding areas, which was adopted by Uvarov. By 1934, this had crystallized into the term *outbreak areas*. This was useful because it pointed to a small number of places where an upsurge of numbers in a resident population sometimes leads to swarms, which may break out in emigration and begin a plague. A resident control service may well control such populations so as to limit upsurges and prevent outbreaks. That is the true early American or Uvarovian strategy of outbreak-area control, applied for the last 30 years to *Locusta* and *Nomadacris*.

With species whose upsurges occur in many and widely scattered places and, as in the Desert Locust, depend on seeding by immigrants rather than a resident population, the conception is stretched too far to be of practical value. To call the places of upsurges *outbreak areas* at all is merely confusing. Certainly upsurges of the Desert Locust should be nipped in the bud, if possible; but that cannot be done by a resident control service controlling a resident population of locusts. The strategy has to be different.

Certainly the area within the limits of invasions of Desert Locusts is not very different from the area within which the species breeds during recessions; the ratio is perhaps two or three to one, contrasted with a ratio of much more than a thousand to one for *Nomanacris*. Of course, all areas include many places where breeding never occurs at all, but that does not affect the essential difference between the types A and B in their extreme forms, as I described them in my first paper (§ 1).





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R. C. Rainey

John Kennedy points out that the original Uvarovian view about controlling outbreak areas of the Desert Locust is still dominant today, and the explanation of that is simple. Since 1967 it has repeatedly proved impracticable to obtain the official approval necessary for the publication of the views expressed in our paper, and opportunities for presenting such views at any meeting concerned with Desert Locust control have also been correspondingly rare. In actual fact, the important differences from Uvarov's original concept which are shown by the Desert Locust (the absence of fixed and permanent outbreak areas, and the continuing appearance or re-appearance of swarms), and to which he himself forcefully directed attention more than 20 years ago (FAO 1956), have continued to characterize subsequent Desert Locust history, which has in addition illustrated further how observations of gregarization lack any special value in forecasting upsurges. Experience has furthermore shown how the nomadic Desert Locust can indeed become unpredictable when these findings are disregarded. In my own view the immense initial value of the Phase Theory as a stimulus to research on the Desert Locust, particularly in the field, has declined for a long time, and for the past decade or two has I think become negative, by postponing more comprehensive studies. It is the relationships in space and time between all the various Desert Locust populations reported, as illustrated in outline for 1963–8 in our figure 2, which provides the inescapable framework for any serious consideration of the population dynamics or of the strategy of the control of this species (and similar considerations would appear to any other pest species showing substantial flight activity). For the further elucidation, interpretation and exploitation of these spatial and temporal relationships, and for evidence of the manner in which airborne radar could transform the central problem of numbers to which Dr Gunn refers, worked examples are now on record; and the Desert Locust could even prove to be the first pest species for which a strategy of total population control becomes demonstrably practicable.

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May I give a little background about the organization concerned with the armyworm problem in East Africa. There is the East African Agriculture and Forestry Research Organization, at Muguga near Nairobi (now the Kenya Agricultural Research Institute), where Peter Odiyo and his warning service provide the coordination of information which is an essential part of the whole programme. There is the International Centre for Insect Physiology and Ecology (ICIPE) with which I am concerned, in Nairobi, which is concerned not with control at all, but with acquiring the necessary fundamental knowledge to enable control programmes to be effective. At ICIPE the armyworm team includes two scientists, Dr Khasimuddin and Dr Personne (who are both here today), with supporting people. Finally, the Desert Locust Control Organization for Eastern Africa, as Ato Adefris has told us, has in the last year assumed an added responsibility for control operations against armyworm (and other pests such as *Quelea*), and have often carried out such operations on an *ad hoc* basis in the past. Also attached now to DLCOEA are Dr Rose, Mr Dewhurst and Dr Maslen, from the Centre for Overseas Pest Research; Dr Rose also has an honorary position in ICIPE so that he is able to coordinate the research work on armyworm in all three organizations. In southern Africa also there are organizations concerned with armyworm, in Rhodesia and South Africa, which I could perhaps ask Dr Blair to outline.

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In southern Africa we run a light trap grid, described by Roome (1974), and one of the species we monitor is *Spodoptera exempta*. An exchange of information takes place between the coordinating countries, and we also send information through to Muguga for collation there. Records of outbreaks of larvae are collated as well as the trap records of moths. Control in southern Africa is left by and large to the individual landowner or farmers, and is not really the responsibility of government in these countries.

D. J. W. Rose

George Popov's question as to the practical implications of the alternative hypotheses for Desert Locust control strategy has relevance also to the armyworm problem, but before commenting on control strategy in relation to the importance of gregarious and non-gregarious phase caterpillars it is necessary to say that phase change in the armyworm may have a different significance to the same phenomenon in locust biology. For example there is no evidence for truly gregarious behaviour in armyworm caterpillars or for the production of a gregarization pheromone. Also a pupal stage intervenes between the caterpillar and the moth stages, and there are no known differences in the readiness to fly or flight durations of populations of moths reared from gregarious or solitary-phase caterpillars. The latter point needs urgent investigation in order to help resolve the question of whether outbreak caterpillars are more likely to generate further outbreaks than similar sized populations of solitary-phase caterpillars. At present the physiological differences that have been found between solitary and gregarious-phase caterpillar and pupal stages give no reason to suppose that phase change is anything more than a stress phenomenon associated with crowding.

The hard facts are that only the crowded caterpillars are conspicuous because of their colour, activity and high density; and that it is only practical to attack these outbreak caterpillars with insecticides. As there is a progression of outbreaks through Africa, there is hope that if the moths emerging in mass from the first outbreaks are eliminated, then the progression will be checked. This strategy has to be tried.

At the same time a clear understanding has to be obtained of the environmental factors that cause concentration of moths at oviposition sites, and that cause high survival of caterpillars so that they become crowded and gregarious.

Professor Joyce's suggestion that swarms of moths may be killed in the air with insecticides is attractive as it may be equally effective against moths from populations of solitary and gregarious-phase caterpillars. However before this tactic can be adopted much more research is needed, with close cooperation between meteorologists, physicists and entomologists.

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